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THE BIOLOGICAL COUNTERPART TO NON-COOPERATIVE GAME THEORY

by

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Recently, Maynard Smith (1982) has published a book entitled "Evolution and the Theory of Games". It is the purpose of this paper to present some thoughts evoked by this publication which may be of interest to the mathematically educated reader. Evolutionary game theory, the subject of the book, is an intriguing new field of biomathematics.

1. Quasi-rational animal behaviour

It is common thinking that mathematical theories almost invariably originated from the natural sciences. Therefore, mathematical methods for the social sciences typically appear as "second-hand" tools that were made available to the economist or sociologist by their original users in physics, chemistry or biology.

Game theory represents an important exception to the rule that there is mainly a one-way transfer of methodology between the natural and social sciences. This branch of applied mathematics was undoubtedly born as a child of economic decision theory, but then was also adopted within the field of evolutionary biology. Today, it even provides some of the most powerful methods for analysing animal behaviour from a neo-Darwinian point of view.

How could this unusual transfer from the social to the natural sciences arise? The history of the concepts involved is all but straight. In 1944, von Neumann and Morgenstern created game theory as a mathematical attempt to deal with the problem of rational decision making in interpersonal conflict situations. The idea of rationality, however, didn't seem to apply to anything other than the human mind (clearly, even the human mind is well known for being an unreliable

source of rationality). It is, therefore, easy to understand why the animal world was not considered a matter of strategic analysis in von Neumann and Morgenstern's work and, for more than two decades, in the subsequent publications.

Even John Maynard Smith, the main initiator (together with George Price) and "ring leader" of biological game theory did his pioneer work under the impression that only the notion of a game as such would be of use to evolutionary theory, but not the classical "solution concepts". These concepts specify what the idea of "rational behaviour" means in mathematical terms.

In their seminal paper, Maynard Smith and Price (1973) pointed out the fact that game-like conflict occurs in nature whenever animals contest for access to limited "resources", such as food, territories or females. They proposed to model animal contests as symmetric bimatrix-games known from non-cooperative game theory. However, they decided to invoke models of natural selection instead of the rationality concept for understanding the logic of observed animal contests. This decision has led to the evolutionary solution concept for symmetric non-cooperative games.

In his recent book, Maynard Smith (1982) gives an excellent survey on how this solution concept applies to a great variety of problems in sociobiology. He convinces the reader that strategic analysis is an essential key for understanding the ultimate evolutionary causes of social behaviour, including cooperation on the one hand and competition on the other.

The book testifies its author's great devotion to applying mathematical ideas to the study of evolution at the phenotypic level. This devotion made Maynard Smith one of the most popular figures in contemporary biology, since it is paired with his talent to make his "sums" intelligible to those scientists who deal with facts rather than with integrals and eigenvalues.

The present essay comments on Maynard Smith's impressive book and discusses some of the mathematical problems it raises. One such

problem is the understanding of the conceptual relationship between non-cooperative game theory and its biological counterpart. This relationship is not fully explained in the book, and it is often misrepresented in the literature. In order to clarify this point, the history of concepts shall be continued in the following paragraphs.

Within the theoretical framework initiated by Maynard Smith and Price (1973), animals are supposed to "play" an "evolutionarily stable strategy" in the game they are involved in. Roughly speaking, this is a strategy such that a population of animals adopting that strategy cannot be "invaded" (via selection) by any other "mutant-strategy" that occurs in this population at a very low proportion.

Here, the underlying assumption is that strategies are heritable traits and - unlike strategies in economic decision theory - not subject to individual cognitive choice. On the other hand, the process of natural selection is now considered as the "decision maker".

The notion of an evolutionarily stable strategy depicts at least one type of "long-term outcome" of an evolutionary process: a population state that is (a) monomorphic (i.e. all individuals play the same strategy) and (b) stable against "perturbations" that are caused by low proportions of animals playing a different strategy. With regard to (b) it should be noted that the term "perturbation" is used in a restricted sense: in a perturbed state, more than one individual is allowed to play a different strategy, but only one different strategy is allowed.

Quite surprisingly, it turns out that the formal characterisation of an evolutionarily stable strategy (ESS) corresponds, up to an additional requirement, to that of a symmetric equilibrium point introduced by Nash (1951). An equilibrium point is a combination of strategies (one for each player) that are individually optimal for each player if he can expect the other players to "stick" to that combination. According to the philosophy of non-cooperative game theory, rational players must play an equilibrium point.

The game theoretic equilibrium property of an evolutionarily stable strategy (ESS) allows us to draw the following striking conclusion: animals performing an ESS behave in a "quasi-rational" way, i.e. they behave as if they were rational Bayesian decision makers. This is astonishing, because animals are not supposed to make any cognitive choice of strategy in the framework under discussion!

The apparatus of non-cooperative game theory, therefore, is highly relevant to animal behaviour, a fact that was not foreseen by the pioneers of evolutionary game theory. Their picture of classical game theory (e.g. Maynard Smith 1976) contained as the main theme the so called maximin-philosophy. This philosophy proposes to choose that strategy that maximises among the "worst possible outcomes".

Perhaps the earliest biological attempt to use game theoretic arguments in the evolutionary context was even based on the maximin philosophy: Lewontin (1964) considered an animal species as a player who plays maximin-strategies against the rest of nature, thereby avoiding species extinction. In a recent paper, Lewontin (1982) admits that Maynard Smith's approach is biologically more convincing than his own previous approach. This is so, since natural selection operates primarily via differences in the viability and the fertility of individuals, but not so strongly via differences in the overall success of local populations. It is a generally held view in modern biology that selection at the level of local populations can hardly counteract selection at the individual level. Therefore, neither a local population nor the entire species represents a "level of aggregation" to which the idea of adaptation by natural selection can be applied directly.

There also are strong reasons why maximin is a doubtful principle for classical games. The most important criticism is that a "maximiner" ignores how likely the different strategic options are to be chosen by a rational opponent. Here, a defendant of maximin would point to the fact that uncertainty exists with regard to these probabilities, since they are unknown. He would claim that one should take into account only those probabilities that are known, like that of hitting a given number with a single throw of a dice. Only in this case there seems

to be a risk that is calculable. However, this attempt to defend the maximin philosophy is based on the unconvincing idea that there exists a clear logical distinction between (a) decision under risk and (b) decision under uncertainty. From a Bayesian point of view this distinction cannot be made, since rationality axioms force a rational individual to form subjective probabilities in every decision situation.

A further problem with maximin was discovered by Aumann & Maschler (1972). They point to differences between applying the principle "globally" to the entire game or "locally" while playing the same game. These differences are annoying, since there is no satisfactory answer to the question of what would be the relevant level to which a decision maker should pay more attention.

No wonder, the main stream of classical game theory has abandoned the maximin-principle in the early fifties, shortly after Nash's introduction of the equilibrium point concept. Today, the principle is only used for two-person zero-sum games as an equivalent "surrogate" of the equilibrium point.

To conclude the discussion of "methodology-transfer" between the social sciences and biology, it should be emphasized again that, contrary to Maynard Smith's original thoughts, not only the classical notion of a non-cooperative game as such, but also the classical solution concept (Nash's equilibrium point) is relevant to evolutionary biology. In his book, Maynard Smith pays almost no attention to this fact, since he wants to avoid to confuse the biological reader by the intricacies of non-cooperative theory. To a biomathematician, however, it is of great interest to know that the body of mathematical knowledge about equilibrium points is applicable to biology with only a few restrictions.

All this does not mean that Maynard Smith simply "sticks to the old way". Probably the most important aspect of what he has added to the previous body of game theory is his new dynamic interpretation of the equilibrium point as a long-term outcome of selection. Furthermore, he

enriched the equilibrium point notion with a supplementary stability condition.

2. Evolutionary games

A well known paradigm of classical game theory is the game of Chicken. This game is played by two human players who drive cars on a collision course. The first one to swerve loses the game. He receives payoff 0, and the opponent receives \$ 200. In case of a crash, both share the \$ 200, but they have an expected cost of \$ 1000 for repairing their bashed in cars. If both swerve, they share the \$ 200 and no cost arises. The following bimatrix game provides a simple formal representation of this contest that was fashionable among American teenagers in the time of James Dean.

	NOT SWERVE	SWERVE	
NOT SWERVE	-900 , -900	200 , 0	(1)
SWERVE	0 , 200	100 , 100	

This symmetric game has a symmetric equilibrium point that prescribes for both players to swerve with probability $9/10$. If both play this mixed strategy, they each receive the expected payoff 90. Note that this is less than they would get if they agreed to swerve with probability 1. However, since there is no force that would bind such an agreement, this lack of commitment power leads to a rational solution which is not Pareto-optimal (an outcome of a game is called Pareto-optimal if the players cannot improve one player's payoff without deteriorating the payoff of another).

The biological interpretation of the game of Chicken is well known as the Hawks-Doves paradigm. This paradigm has a central place in Maynard Smith's book, but he omitted to mention its conspicuous analogy with Chicken. In the Hawks-Doves game, two animal opponents compete for

access to an indivisible resource. Both belong to the same species. Furthermore, they are equally matched.

In order to get the resource, the competing animals may either escalate (not swerve) to an injurious fight, or just display (swerve) in order to reach a peaceful settlement. In the latter case, both opponents have an expected "payoff" which corresponds to half the resource value. If one animal escalates and the other displays, the escalating individual gets the resource at no "cost" and the opponent neither loses nor gains anything. If both escalate, their expected payoff is half the resource value minus the cost of injury.

It is easy to see that the Chicken-bimatrix (1) depicts such a contest if the resource is worth 200 units on an appropriate "utility-scale", and if injury inflicts a "cost" of 1000 units. But what is the exact interpretation of payoffs, i.e. what utility-scale is relevant to biological games? Unlike classical game theory, which has to struggle with an individual's subjective measure of success, evolutionary game theory relies on an objective measure of an individual's success. In the biological context, up to a constant factor a payoff corresponds to the change in expected Darwinian fitness (reproductive success) that results from playing the game.

Now, suppose that a symmetric bimatrix game like Hawks-Doves (Chicken) is played generation after generation in a population. Suppose further that opponents are paired at random. What characterises, then, a strategy p that is adaptive in a population of animals playing it? A strategy p is adaptive if in this population no other strategy would have a higher expected Darwinian fitness. Let $E(p,q)$ denote the expected payoff for playing p against q in the symmetric game. Obviously, in order to be an adaptive response to a world of look-alikes, the following must hold for p :

Equilibrium condition: p is a best reply to p , (2)
i.e. $E(p,p) \geq E(q,p)$ for all strategies q .

To put it in classical game theoretic terms, this condition characterises the equilibrium strategy of a symmetric equilibrium point.

In the Hawks-Doves (Chicken) game (1), there is only one strategy that has the equilibrium property, namely the rational solution to escalate (not swerve) with probability $1/10$. Let us call this specific mixed strategy the "occasional aggressor".

The question now is whether a population in which all individuals play "occasional aggressor" would be driven back to that state after "perturbation" by a small proportion of individuals playing another strategy q . Assuming "decent" properties of the underlying genetics, this may seem obvious because it is adaptive to play occasional aggressor in the population we are faced with. However, if a mixed strategy p satisfies (2), every other strategy that mixes over the same pure strategies (or a subset of them) is also a best reply to p . This is the well known fundamental property of best reply strategies. Therefore, in a population playing the equilibrium strategy "occasional aggressor", every other strategy including "escalate" and "display" is also adaptive! Why couldn't one of those equally adaptive strategies invade the population with a little initial help by random drift and a subsequent selective advantage in the perturbed population state? The following stability condition for a strategy p guarantees that such alternative adaptive strategies are selected against if they increase to a small fraction of the population:

Stability condition: (3)
 if another strategy q is also a best reply to p ,
 that is if $E(q,p)=E(p,p)$, then $E(p,q) > E(q,q)$.

This condition was unknown to classical game theory. No such requirement has been used in the theory of rational decision making so far.

Now, we return to our example. The equilibrium strategy "occasional aggressor" of the Hawks-Doves game (1) has the stability property (3). It represents the most famous specimen of an evolutionarily stable strategy (ESS). In a symmetric bimatrix game, a strategy p is called evolutionarily stable if it satisfies both the equilibrium condition (2) and the stability condition (3). Maynard Smith defines an ESS in a slightly different but equivalent way. His formulation makes it less

explicit that an ESS corresponds to a symmetric equilibrium point with an additional characteristic.

Note that two animal opponents playing the ESS "occasional aggressor" do not perform the "best job" for the species, since both of them could simultaneously achieve a higher payoff if they played "display" (swerve). Whereas in the human world contracts may sometimes provide the commitment power needed to stabilise the Pareto-optimum in which both display, no similar mechanism can be found in the animal world. This is one of the reasons why cooperative game theory seems, at least up to now, irrelevant to biology. It must be emphasized at this point that the distinctive feature with regard to cooperative versus non-cooperative game theory is not the interest in cooperation versus the interest in non-cooperation. In contrast to the misleading terminology, the distinction can be described as follows. Cooperative game theory assumes some degree of cooperation, since its solution concepts "blindly" rely on Pareto-optimality. Conversely, non-cooperative game theory and sociobiology always try to explain cooperation .

3. A bunch of problems

Evolutionary games and evolutionarily stable strategies exhibit a few peculiarities and pose a number of problems that deserve a biomathematician's attention. A short survey will be given in the remainder.

Looking at the game of Chicken again, the question arises how to model the conflict if one of the opponents has a small fragile car, whereas the other is equipped with a big car with very solid bumpers. Biologically speaking, this could be analogous to the conflict between a juvenile deer and its adult rival. There exists, then, an obvious asymmetry between the two players. Classical game theory would simply model the conflict as an asymmetric bimatrix game in which the matrices no longer are the transpose of each other. However, Maynard Smith's definition of an ESS only refers to symmetric games. Is there a need for asymmetric evolutionary games?

My view on this problem is that an evolutionary conflict should typically be modelled as a symmetric game. This is more than an

artificial symmetrization, since there is no reason why an adult red deer and its juvenile conspecific opponent should not carry the same genotype and thus play the same inherited strategy. Note that this strategy may assign different actions to the roles "adult" and "juvenile". Sometimes, the evolutionary game can be decomposed into subgames on which an evolutionarily stable strategy "induces" strong asymmetric equilibrium points (Hammerstein 1981). In a number of biological publications, the reader is confronted with immediate presentations of asymmetric subgames. These presentations are lacking explicit statements about the actual evolutionary game. The caveat must be given here that implicit assumptions on the informational structure of the evolutionary game are involved in such cases. These assumptions are notoriously violated in conflicts with incomplete information about roles, such as the asymmetric war of attrition studied by Hammerstein & Parker (1982).

Particular problems with the symmetry of evolutionary games are met if one tries to extend the concept from bimatrix games to extensive games (those trees that grow in game theory books). Selten (1983) gives an intriguing simple example where two biologically very different conflicts are represented by the same extensive game. He draws the conclusion that the classical extensive form of a game has to be enriched with an additional "symmetry" that maps information sets and moves onto their "natural image". Otherwise ambiguity would exist as to whether two opponents play the same strategy or different ones.

There are more delicate problems with extensive evolutionary games. If one adopts Maynard Smith's conditions for evolutionary stability in the context of extensive games, this evokes a disaster: many strategies that seem to be biologically appealing "candidates" for an ESS fail to satisfy the formal conditions; furthermore, many interesting games do not have an ESS at all. This is so because the equilibrium paths in extensive games typically do not reach all information sets. A mutant strategy that behaves differently from an equilibrium strategy at these unreached parts of the game is an alternative best reply to the equilibrium strategy. Nothing prevents the initial spread of such a mutant by means of random drift.

To give an example, consider the famous Prisoner's Dilemma. This is a two-person game in which the opponents may either "cooperate" or "defect". In the single shot game, it is for both opponents a strictly dominating strategy to defect. However, the repeated Prisoner's Dilemma has one equilibrium point, among many others, in which both players play "Tit for Tat". Tit for Tat is to cooperate in the first period and then match the opponent's move of the previous period for the rest of the game. Axelrod & Hamilton (1981) claim that Tit for Tat is an ESS, and Maynard Smith shares their view in his book. He even discusses the "basin of attraction" of Tit for Tat. However, according to the definition of an ESS in Maynard Smith's book, Tit for Tat is not an ESS. This is obvious, since "always cooperate" and many other strategies are best replies to Tit for Tat that violate the stability condition (3). On the other hand, "always defect" is an ESS, but this is not what biologists get so excited about.

Selten's (1983) framework of extensive evolutionary games gives us hope to reestablish the idea that cooperation is evolutionarily stable in the repeated Prisoner's Dilemma. He defines a somewhat weaker notion of a limit-ESS as the limit of ESS's (à la Maynard Smith) of a sequence of perturbed games. The limit-ESS is related to the perfect equilibrium point of classical game theory. Probably, a strategy similar to Tit for Tat, but somewhat more complex, is a limit-ESS for the repeated Prisoner's Dilemma.

A further problem area is the modelling of selection. Originally, selection equations that describe exact "parthenogenetic" inheritance (that is: no sex and no recombination), have been used as the dynamic background of evolutionary game theory. These equations describe at the phenotypic level what population geneticists would call "frequency dependent selection". Evolutionary game theory shares a common interest with population genetics in analysing the complicated effects of frequency dependent selection. However, either discipline focusses its interest on a different level: game theory is subtle with the strategic conflict at the level of the individual and crude with the genes; conversely, population genetics is more subtle at the genetic level. A full marriage of both would impose too many conjugal problems. Note, however, that some serious attempts have been made to

analyse under what condition a sexually reproducing population should be expected to play an ESS (e.g. Eshel 1982, Hines 1982). Furthermore, a field where some genetics seems unavoidable is that of games between relatives. Surprisingly, only very few articles have been concerned with these games.

There is one chapter in Maynard Smith's book which is not easy to digest for a mathematician. This chapter deals with the evolution of learning and makes a mathematical attempt to identify "evolutionarily stable learning rules". The game learning process that apparently fascinates Maynard Smith is Harley's (1981) learning rule. This is a stochastic process which is more difficult to analyse than the selection equations that underly evolutionary game theory! Even if one accepts, for this brief discussion, Harley's central argument that an evolutionarily stable learning rule should asymptotically have the so called "relative payoff sum property", this condition does not single out Harley's specific learning rule. Probably, many learning rules have this property, such as the game learning process known as the "method of fictitious play" (Brown 1951, Robinson 1951). For further discussion see Selten & Hammerstein (1984).

The problem that too many solutions exist that satisfy the mathematical conditions used for picturing evolutionary stability is also very likely to occur in many extensive games. Recent work in progress shows that if games similar to Hawks-Doves are played repeatedly between the same two opponents, a great variety of alternative evolutionarily stable strategies exists. This kind of problem is known to classical game theory and has led to the theory of equilibrium point selection. I do not think that this theory is applicable to biology. This seems to be a point of divergence between the rationality concept of decision theory and the quasi-rationality that occurs in evolutionary games.

After all these critical comments, a final word about the book by Maynard Smith: there can be little doubt that the theory he outlines has had an extremely stimulating influence on evolutionary research in animal behaviour. This is largely due to Maynard Smith's attitude of spending more time in communication with empirical biologists than

in petty mathematical details. Thank God, he still leaves us theorists a lot of homework to do!

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